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THE QUESTION OF REVERSAL OF ASYMMETRY IN THE REGENERATING CHELÆ OF CRUSTACEA.

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During the summer of 1909 while at the Tortugas Laboratory of the Carnegie Institution I undertook a further analysis of the reversal phenomenon in regenerating specimens of the genera *Alpheus* and *Synalpheus*. These small crustacea commonly called snapping shrimp, on account of their habit of snapping the large chelæ with such force as to produce a surprisingly loud noise, are abundantly found in the "logger-head" sponge and in the holes of disintegrating coral rock on the Tortugas reefs. There are a number of species five of which, *Alpheus formosus* and *armillatus* and *Synalpheus minus* and two other unidentified species of *Synalpheus*, were employed in these experiments.

The several species differ in size and body color but are essentially similar in general structure. The first pair of appendages is decidedly asymmetrical in both sexes. One member of the pair, either the right or the left, is extremely large, in some cases being more than half the size of the body itself. The general type of this chela in the five species follows more or less closely the description given by Wilson,¹ for the great chela of *Alpheus heterochelis*. It is greatly rounded or swollen with transverse grooves on either side of the propodus, varying in depth with the species, and presents characteristic color patterns being tipped with a lively rose color in *Synalpheus minus* while in the other species it is bluish, dark or brown. On the concave side of the dactylus is a swollen knob forming the "hammer" which fits into a corresponding socket on the outer side of the propodus claw. By extending the dactylus and then suddenly snapping the claws together the "hammer" is forced into the socket with the surprisingly loud sound.

Wilson's description further applies in that the large chela has essentially the same structure in both sexes, while the small

¹Wilson, E. B., "Notes on the Reversal of Asymmetry in the Regeneration of the Chelæ in *Alpheus heterochelis*." BIOL. BULL., IV., pp. 197-210, 1903.

chela shows characteristic sexual differences, we shall be mainly concerned, however, with the fact that the small chela is always typically different from the large chela in shape as well as in size.

Przibram¹ discovered that in several species of *Alpheus* after the removal of the large chela a chela of the small type regenerated from its base while the small chela of the opposite side metamorphosed or developed into a great chela of typical form at the following moult. In other words, the asymmetry was reversed. Further, when both first chelæ are removed they regenerate in their original conditions, no reversal following.

Zeleny² found an exactly similar phenomenon to occur after removal of the functional operculum in the worm, *Hydroides*. In this case the rudimentary operculum of the opposite side develops into a functional operculum while a rudimentary organ regenerated from the base of the former functional one. The principle involved in this reversal phenomenon is doubtless the same as that in the crustacea.

Przibram³ later found a similar reversal to occur in other species of crustacea, while in others the removal of either chela is followed by the regeneration of one of the simpler or smaller type without a regulatory change taking place in the uninjured chela of the other side. In still other cases, as for example the lobster, *Homorus*, a chela similar to the one removed invariably regenerates whether the original chela was a large crusher claw or the slender nipping claw.

The crustacea thus present a series from those forms which regenerate appendages of the type of the ones removed, others which regenerate appendages of the simpler type without a compensatory change taking place in the uninjured chela, and finally such forms as *Alpheus* in which the simpler type of chela is regenerated after the removal of the more specialized chela while the uninjured small chela develops into the more modified type,

¹Przibram, H., "Experimentelle Studien uber Regeneration," *Arch. fur Entw.-Mech.*, XI., 1901.

²Zeleny, C., "A Case of Compensatory Regeneration in the Regeneration of *Hydroides dianthus*," *Arch. fur. Entw.-Mech.*, XIII., 4, 1902.

³Przibram, H., "Experimentelle Studien über Regeneration, II.," *Arch. für Entw.-Mech.*, XIII., 1901-1902; "Equilibrium of Animal Form," *Jour. Exp. Zool.*, V., p. 259, 1907-1908.

and thus by a sort of compensatory regulation the animal's asymmetrical condition is quickly reestablished.

Wilson repeated Przibram's experiments on *Alpheus heterochelis* with similar results, but carried the experiments further, hoping to analyze the factors concerned in the reversal process. After removing the great chela the nerve trunk leading to the small chela of the opposite side was clipped in order to test whether there was a nervous control determining the growth of the small chela into a large one. After such an operation the small chela was generally thrown off and only two specimens are said to be beyond question, yet "one of these did not moult quite normally and the other not at all." The evidence, then, does not warrant conclusions as to the cause of reversal of asymmetry in the chelæ. Wilson finally believes that the initial factor that sets in motion the complex process of differentiation of which either side is capable, is primarily only a difference in the amount of material on the two sides. "Removal of the large chela obviously reversed the asymmetry in respect to the amount of material and must, temporarily, at least, lead to a functional nervous difference." Such a suggestion may easily be submitted to experimental test, for example, after removal of the large chela from one side of the body if several posterior appendages be removed from the other side the greater amount of material may still remain on the original large chela side. Fig. 1, *A*, illustrates the operation. Under these conditions will a large chela regenerate from the stump of the old one, instead of arising by a growth of the small first chela of the opposite side?

Again, the proposition may be tested by removing both the great and small chelæ of the first pair and in addition amputating several legs on the side of the large chela; the operation is illustrated by Fig. 1, *E*. The greater amount of material is now on the original small chela side; will this extra amount cause a great chela to regenerate from the small stump instead of from the stump of the great chela which is on the side with less material?

Lastly, when only a portion of the great chela is amputated does it regenerate in the original condition or become a small chela, while a large chela appears on the opposite side through a metamorphosis of the small first chela?

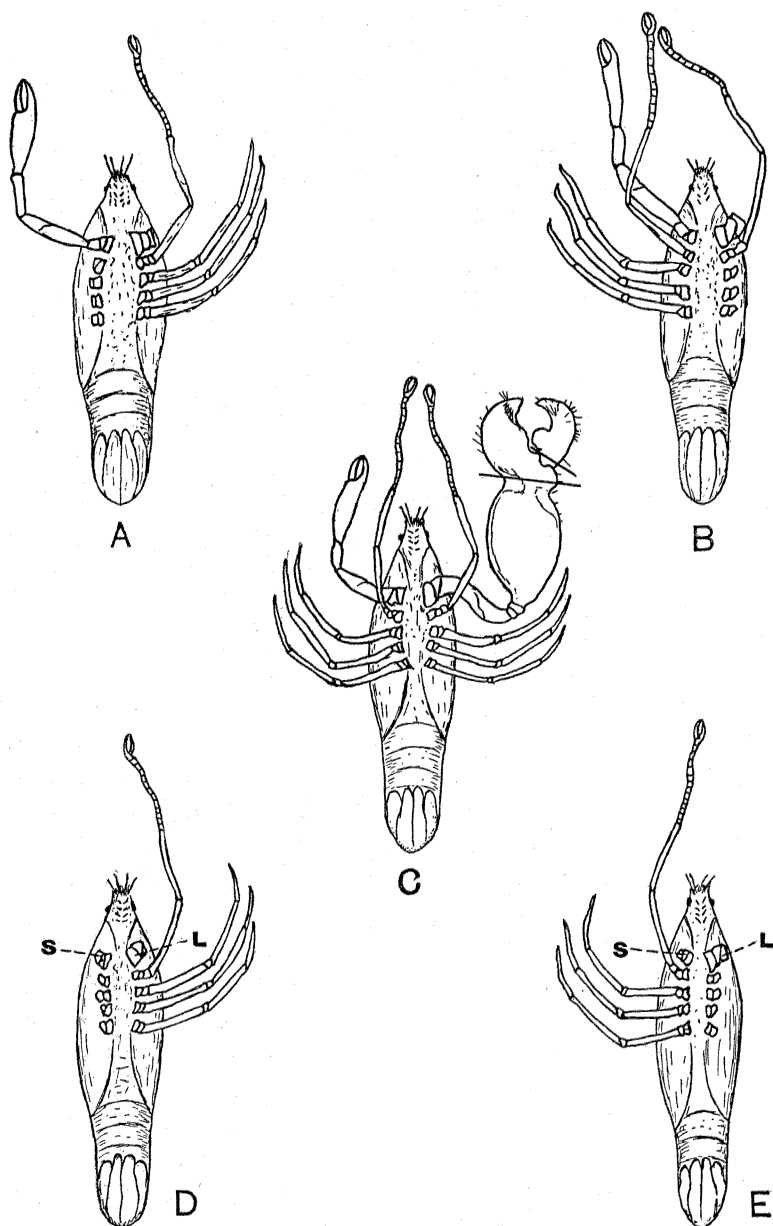


FIG. 1. Diagrams illustrating the manner of operation in the several experiments. *A*, removal of the great chela and the posterior appendages of the opposite side, causing the larger amount of material to still remain on the great chela side; *B*, the opposite operation as a control; *C*, the heavy lines show the places at which portions of the great chela may be cut away without reversal; *D* and *E*, removal of both first chelae and posterior appendages from either the small, *D*, or great, *E*, chela side, to determine the influence of the lateral amount of material on the regeneration of the first chelae; *L*, large chela stump; *S*, small chela stump.

Aiming towards an answer for these questions a number of experiments were performed the results of which may now be considered.

Fifty healthy specimens representing the five different species were selected, and tested as to their tendency to reverse the asymmetry of the first pair of chelæ during the regeneration following the removal of the great chela. Without exception all of the specimens responded as Przibram had found, a small chela regenerated from the stump of the original great one and the small chela of the opposite side metamorphosed into a great chela. Forty of the specimens favorably survived the experiments.

FIRST SERIES.

Nineteen individuals had the great chela removed and in addition a number of posterior appendages were amputated from the opposite or small chela side, so as to allow the greater mass of material to remain on the original great chela side. The operation is illustrated by Fig. 1, *A*, and the opposite or control operation by Fig. 1, *B*, or specimens 10, 12 and 31 in the table. Referring to the table the results of such an experiment may be ascertained.

The left side of the table gives the date of the operation, the number of the specimen, and the appendages removed are indicated by *x*, *G* and *S* in the first appendage column indicate the great and small chela. The right side of the table gives the time of moulting and the manner of regeneration, the *r* signifies a new or regenerated leg, *G* and *S* in the first appendage column again indicate the great and small chela. The horizontal lines of the table are so arranged that the appendages on the right side of an individual are given immediately above those on the left of the same animal, *e. g.*, specimen 1 had the great chela and the second leg removed from the right side and the fourth leg from the left side in the first instance. Each specimen, as the table shows, was operated upon a second time during the experiments.

Of the nineteen cases having the great chela removed from one side and other appendages than the first chela from the opposite side the small chela, even though it was on the side of less mate-

rial, retained the power to grow into a large chela of typical form in seventeen cases. One of these cases, specimen 23, is remarkable, since at the first operation the small chela which was on the left side and the other four left appendages were all removed and regenerated at the next moult. After this moult the large chela of the right side was amputated along with the four posterior legs of the left side, thus leaving only the regenerated small chela on the *left side* while the four posterior legs remained on the right side. Nevertheless, the left small chela grew into a great chela and the four more posterior left appendages regenerated for the second time. The case seems an extreme test of the power of one side to regenerate all of its posterior legs for a second time and in addition to change the first chela from the small to the large size and type. Specimen 25 further indicates this remarkable power of the side of the individual with less material to replace all lost parts and at the same time increase the size and type of its first chela.

The remaining two of the nineteen cases, specimens 9 and 18, present the first chelæ equal in size after the moult following the second operation. Specimen 9 had in the first case the great chela removed from the right side and the third, fourth and fifth appendages from the left side. The greater amount of material was, therefore, still on the right side, yet the small first chela of the left side became larger after the moult. The second operation removed the great left chela and the second, third, fourth and fifth legs of the right side. After the moult all of the amputated legs were regenerated but the regenerated left first was small, and the right first appendage had not increased in size. Thus the first pair were symmetrical in respect to size yet the right first or old chela had slightly approached the large chela type. The specimen 18 responded in a closely similar fashion.

The type of the chela is equally, if not more, important than the size since Przibram found the chelæ to be of almost equal size in some cases but of reversed type, and the great type invariably increases in size at the following moult.

The experimental evidence in the first case, then, does not support the idea that the side with most appendage material

has most power to produce a great chela of typical size and form. The tendency is to produce a chela of the great size and type from the uninjured first chela, even though this be the original small chela and is located on the body side which has suffered the loss of all other walking appendages. There seems to be no evidence from these experiments to suggest a bilateral distribution of growth energy accompanying distribution of appendage material.

SECOND SERIES.

The question of a bilateral distribution of growth energy related to, or accompanying, the amount of appendage material on a given side was further tested in the following manner. Fifteen specimens were operated upon so as to remove both chelæ of the first pair. It was known that when only these two chelæ were removed that they regenerated in their original condition, a large chela from the base of the original large chela and a small chela from the opposite side. If now in addition to the removal of the first pair of appendages a number of more posterior appendages also be removed from the large chela side, this side will have less appendage material remaining and is, therefore, called upon to regenerate a greater amount of material to replace the posterior legs. Will this side of the body at the same time be more capable of producing a first chela of larger size and specialized type than the opposite side which is called upon to replace only the first chela? Such an operation is illustrated by Fig. 1, *E*, and Fig. 1, *D*, forms a control experiment in which the additional appendages are removed from the small chela side.

The usual idea of regulation would require the side with only the first leg removed to regenerate a large chela while the other side replaced the several posterior legs and produced a small first chela. It is found on examining the table that after an operation to remove both first chelæ and one or more posterior legs on *either* the great or small chela side that six of fifteen specimens regenerated the chelæ of the first pair equal in size, not one individual reversed the type of the first chelæ, and eight regenerated the first chelæ in their original condition as though no additional appendages had been removed. One specimen died before the experiment was completed.

Considering the six specimens that regenerated the chelæ of the first pair equal in size it is important to find that four of these cases, specimens 16, 20, 21 and 39, had the larger number of posterior appendages removed from the side of the original small chela and not from that of the large chela, so that the greater amount of material remained on the large chela side. Such operations were intended as a control for the results following the removal of posterior appendages from the large chela side. Although in these four specimens there was more material on the original large chela side and this side was called upon to regenerate fewer appendages it failed to produce a great chela from the stump of the original one.

In specimen 16 the first chelæ remained equal in size and were both of the small chela type after a second moult. The left chela was then removed and after the next moult the right developed into a great chela and the left again regenerated small. Both first chelæ in specimens 20 and 21 were also of the small chela type, while in specimen 39 the small chela failed to regenerate at the first moult after the operation though a chela of the small type regenerated from the base of the great chela and remained small while the right small chela regenerated at the next moult.

Specimens 31 and 32 had both first chelæ and a number of appendages, four and three, on the great chela side removed. After the moult following the operation the first chelæ were equal in size. Yet again specimens 27, 35 and 38 were operated upon in an identical fashion and after the moult they were able to produce a great chela from the original great chela stump even though this side was called upon to regenerate three other appendages.

Of the fifteen cases tried, therefore, eight regenerate their first chelæ in the original condition of asymmetry while six regenerate the chelæ of the first pair equal in size and usually similar in type whether additional appendages are amputated from the great chela side or from the small chela side. Such a fact would seem to indicate that the amount of appendage material present on either side is an unimportant factor in determining the type of the first chela on a given side, and it seems to show further that there is no clearly evident bilateral distribution of growth energy in these regenerating specimens.

TABLE I.

THE EFFECT OF REGENERATION ON THE ASYMMETRICAL CONDITION OF THE FIRST PAIR OF CHELÆ IN FIVE SPECIES OF *Synalpheus* AND *Alpheus*.*

Date of Operation.	Specimen Number.	Appendages.					Date of Mout.	Appendages Regenerated.					Remarks.
		1	2	3	4	5		1	2	3	4	5	
May 24	1 R	Gx	x				June 4	Sr	r				The small chela increases in size and changes its form to type of great chela.
	1 L			x			G			r	r		
June 6	1 R	Gx	x	x	x		June 16	G		r	r	r	
	1 L						Sr						
May 24	2 R	Sx	x		x		June 1	G			r		The third and fifth are only short buds, not fully regenerated.
	2 L	Gx	x				Sr	r					
June 6	2 R	Gx	x	x		x	June 15	Sr	r	r		r	
	2 L		x	x			Gr	r					
May 24	3 R			x	x		May 30	G		r	r		Only the dactyl removed and regenerated.
	3 L	Gx	-				Sr						
June 6	3 R	Gx					June 15	S					
	3 L						Gr						
May 24	4 R	Gx					May 29	Sr					Also moulted one day after the operation but had not regenerated
	4 L						G			r	r	r	
June 6	4 R	Gx		x	x	x	June 13	G		r	r	r	
	4 L						Sr						
May 24	5 R	Gx					June 4	G					Failure of third and fourth legs to regenerate might account for first chela becoming large.
	5 L	Gx	x				Sr	r					
June 6	5 R	Gx	x	x	x	x	June 13	Sr	r				
	5 L		x				G	r					
May 24	6 R	Sx	x	x	x		June 1	Sr	r	r	r		Moulted few hours after operation on May 24 and right first chela began to increase in size.
	6 L	Gx					Gr						
June 6	6 R	Gx	x	x	x	x	June 12	G	r	r	r	r	
	6 L						Sr						
May 24	7 R	Gx					June 3	G					Also moulted two days after operation but no regeneration.
	7 L	Gx		x			Sr		r				
June 6	7 R	Gx					June 13	Sr					
	7 L			x	x	x	G		r	r	r		
May 24	8 R	Gx					May 30	Sr					Moult followed so soon after operation that left first chela had not attained full size, but did so after a few days.
	8 L						G						
June 7	8 R	Gx			x	x	June 14	G			r	r	
	8 L						Sr						
May 24	9 R	Gx					May 29	Sr					Also moulted 2 days after operation. Right first somewhat similar to great chela type but small.
	9 L			x	x	x	G		r	r	r	r	
June 7	9 R	Gx		x	x	x	June 14	S	r	r	r	r	
	9 L						Sr						
May 24	10 R	Gx	x		x	x	May 30	G					
	10 L						Sr	r			r	r	

TABLE I.—*Continued.*

Date of Operation	Specimen Number.	Appendages.					Date of Moul.	Appendages Regenerated.					Remarks.
		1	2	5	4	5		1	2	3	4	5	
June 7	10	R L	Gx	x			June 14	Sr	r				Operated immediately after a moult on June 7.
					x	x		G		r	r		
May 24	11	R L	Gx				May 30	G		r	r		
June 7	11	R L	Gx	x			June 13	Sr	r				
				x	x	x		G		r	r	r	
May 24	12	R L	Gx				June 2	Sr					
				x	x	x	June 15	G	r	r	r		
June 7	12	R L	Gx				June 15	G					
				x	x	x	May 29	Sr		r	r	r	
May 24	13	R L	Gx				May 29	Sr					Died after operation.
								G					
June 7	13	R L	Gx										
May 24	14	R L	Gx				June 1	Gr					o Only the dactylus and index cut from great chela, no reversal.
June 7	14	R L	Gx				June 14	Gr					
May 24	15	R L	Gx				June 3	Gr					Second operation and result the same as first.
								Sr					
June 7	15	R L	Gx	x			June 15	Sr	r				
				x				G		r			After a second moult on June 7 the first chelae were still of equal size.
May 24	16	R L	Gx				May 31	Sr					
					x	x		Sr		r	r		
June 7	16	R L	Ex				June 13	G					The left first chela was removed and right became large and left regenerated small.
								Sr					
May 25	18	R L	Gx				June 1	G		r			
June 7	18	R L	Gx				June 14	Sr					Pincer of left first seems slightly nearer the great chela type.
				x	x	x		S		r	r	r	
May 25	19	R L	Gx				June 3	Sr					
June 8	19	R L	Sx				June 15	G		r			
				x	x	x		Gr		r	r	r	
May 25	20	R L	Gx				June 6	G		r	r	r	
June 8	20	R L	Gx				June 19	Sr					Both first chelae of the small type and equal in size.
				x	x	x		Sr			r	r	
May 25	21	R L	Gx				May 30	G	r		r	r	
June 8	21	R L	Gx	x			June 13	Sr	r				Both first chelae of equal size and small type.
				x	x	x		Sr	r		r		
May 25	23	R L	Sx	x	x	x	June 4	G	r		r	r	
June 7	23	R L	Gx				June 15	Sr		r	r	r	Second regeneration of all posterior left legs, yet left first became large chela.
				x	x	x		G	r	r	r	r	
May 25	25	R L	Gx				June 1	G		r	r	r	

TABLE I.—Continued.

Date of Operation.	Specimen Number.	Appendages.					Date of Molt.	Appendages Regenerated.					Remarks.
		1	2	3	4	5		1	2	3	4	5	
June 10	25	R L	Gx Sx	x	x x	x	June 17	Gr Sr	r	r	r	r	Again second regeneration on one side yet first chela of this side becomes large.
May 25	26	R L	Gx Gx	x			June 6	G Sr		r			
June 10	26	R L	Gx Gx		x x	x							Did not moult the second time.
May 25	27	R L	Gx Gx	x	x x	x	June 4	G Sr	r	r	r	r	
June 10	27	R L	Gx Sx	x	x x	x	June 17	Gr Sr		r	r	r	
May 25	28	R L	Gx Gx			x	June 2	Sr G				r	
June 8	28	R L	Gx Gx	x	x x	x	June 14	G Sr	r	r	r	r	Second pair of legs regenerated shorter than usual. Moulded day before the operation.
May 25	29	R L	Gx Gx				June 6	Sr G					
June 8	29	R L	Gx Gx		x x	x	June 16	G Sr		r	r	r	
May 25	30	R L	Gx Gx	x		x	May 29	G- o	r			r	
June 10	30	R L	Gx Sx		x x	x							Moult followed so soon after operation that little increase in right chela, no regeneration of left, after second moult June 7 condition complete Died June 16 without moulting.
May 25	31	R L	Gx Gx	x	x x	x	June 3	G Sr	r	r		r	
June 10	31	R L	Gx Sx	x	x x	x	June 18	Sr Sr	r	r	r	r	First chelæ equal in size and of small type.
May 25	32	R L	Gx Gx		x x	x	May 31	G Sr		r	r	r	
June 10	32	R L	Gx Sx		x x	x	June 15	Sr Sr		r	r	r	Both first chelæ smaller than normal but of equal size.
May 25	33	R L	Gx Gx	x	x x		May 30	G Sr	r	r	r		
June 10	33	R L	Gx Sx	x	x x		June 16	Gr Sr	r	o	o		Failure of 3 and 4 to regenerate may account for first chela's growth.
May 25	35	R L	Gx Sx		x		May 29	Sr G		r			
June 8	35	R L	Gx Gx	x	x	x	June 14	Sr Gr	r	r		r	Left first chela great though regenerating three other legs on same side. Also moulted 2 days after operation.
May 25	36	R L	Gx Gx		x x		June 3	Sr G		r	r		
June 8	36	R L	Gx Gx		x x		June 15	G Sr		r	r		Moulted again June 6.
May 25	37	R L	Gx Gx		x x		May 30	G Sr			r	r	
June 8	37	R L	Gx Sx	x	x x	x	June 15	Gr Sr	r	r	r	r	

TABLE I.—*Continued.*

Date of Operation.	Specimen Number.	Appendages.					Date of Moul.	Appendages Regenerated.					Remarks.
		1	2	3	4	5		1	2	3	4	5	
May 25	38 R						May 30	G					Also moulted June 9 day after operation.
	L	Gx	x	x	x			Sr	r	r	r		
June 8	38 R	Gx	x	x	x		June 15	Gr	r	r	r		
	L	Sx						Sr					
May 25	39 R	Sx	x	x			June 6	o	r	r			First chelæ finally regenerated equal in size and remained so after next moult Moulded again June 6.
	L	Gx			x			Sr			r		
	39 R						June 14	Sr	r	r	r		
	L												
May 25	40 R	Sx					May 30	Sr					
	L	Gx			x	x		Gr		r	r		
June 8	40 R	Sx			x	x	June 15	Sr		r	r		
	L	Gx						Gr					

Each specimen was operated upon twice as indicated. R and L following the specimen number signifies right and left sides of the animal; G indicates the great and S the small first chela; x indicates the appendages removed and r the appendages regenerated.

THIRD SERIES.

Finally, an attempt was made to determine how large a portion of the great first chela might be removed without causing it to regenerate small; or to cause the small chela of the opposite side to grow into the great type. When a large portion of the chela was quickly clipped off with sharp scissors or a knife the remaining portion was soon thrown off at the breaking joint. The only successful operations consisted in the removal of the dactylus or most distal segment which forms part of the claw, and in the removal of the entire pincer or dactylus and distal end of the propodus, as is indicated by the lines drawn across the chela in Fig. 1, C. In the last case a stump-like appendage without a pincer remains.

Following either of these operations the great chela was fully reformed or renewed at the next moult, no reversal taking place.

A small portion of the great chela may then be regenerated in its original form. When the entire chela is removed the small chela of the opposite side invariably grows into a great chela and a small chela regenerates from the stump of the original great one. This reversal of asymmetry may be shifted back and forth for a number of times and occurs in a manner as decidedly pronounced after several operations as it does after the first.

CONCLUSIONS.

The power to reverse the asymmetry of the first chelæ when regenerating a great claw in *Alpheus* does not seem to be closely associated with a difference in the amount of material on the two sides of the body nor with a bilateral distribution of growth or regenerative energy.

Although in certain cases there seems to be a tendency to regenerate the chelæ of the first pair equal in size and similar in type, such a tendency is manifest under conditions so varied in respect to the bilateral distribution of appendage material and call upon the powers of regenerative energy that the present conclusion is warranted. The amount of material on a given side of the animal, or the amount of regeneration required of this side are negative factors in determining the ability of the side to produce a great chela instead of a small one.

NAPLES, July 5, 1910.